A HISTORY AND INVESTIGATION INTO THE FLUCTUATIONS OF *POLYGONIA C-ALBUM* L.: THE COMMA BUTTERFLY

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Causal theories

Several chroniclers put forward conjectures as to why the Comma had fluctuated so greatly in range and numbers, with most concentrating on climate; some other elements, such as loss or change of habitat, were quickly eliminated – "the places it frequented remain practically unaltered throughout the country" (Frohawk, 1914). Also "there is no suspicion of extermination by over-collecting, nor of destruction by fire or flood" (Barrett, 1893). It was thought that the answer might lie "in effects produced upon the atmosphere by increase of population, or by products of combustion, whether from houses, factories, or railway engines" (*loc. cit.*) but there is no correlation between the distributions of *c-album* and a recent quantitative map of atmospheric pollution (Dobson, 1979) – and later national pollution levels were considerably higher than those of last century. In Kent it was thought that the butterfly's decline was "certainly not due to collectors, and is possibly due to altered agricultural conditions" (Bull, 1897) but, as will be shown, this was not the case in this particular instance.

The large-scale expansion of range ceased for a few years after 1935 and there were two events that could have contributed to this interruption; entire broods of larvae of the Comma's near relatives *A. urticae* and *I.io* are known to have been eaten by the inordinately high numbers of wasps prevalent during 1935 (Fletcher, 1936) and there was a severe frost on May 17th which was said to have killed all butterflies on the wing at the time (Tulloch, 1936) and larvae were also killed. However, there is no evidence that *c-album* was adversely affected in other great wasp years or by other late frosts.

The insect was apparently not especially prone to attacks by parasites, although *Pimpla flavonotata* Holm. and *Pteromalus puparum* Swed. have been bred from the early stages (Buckler, 1885) and its near relative *A. urticae* is sometimes heavily affected (Beirne, 1955).

Generally, it is thought that birds do not significantly affect numbers; the spine protected larvae of *c-album* are unpalatable

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when full grown but they are vulnerable to avian attack during early instars (Carrick, 1936). As an adult, the Comma has been specifically ignored by a Spotted Flycatcher (*Muscicapa striata*) whilst taking *I.io* L. (White, 1953), and yet eaten by Sparrows (*Passer domesticus*) (Warry, 1961). Insectivorous birds and especially Sparrows did increase over the years of the butterfly's decline but no corresponding decrease has taken place during the years of expansion.

It has been suggested that the butterfly declined relatively recently in the New Forest because the "over-planting of conifers has led to the disappearance of sallow in the ridings" (Fraser, 1961), thereby leading to a paucity of bloom on which the adults were thought to almost exclusively feed after hibernation. Even if true, this effect would only operate locally.

The hop as foodplant

Some 40 different insects have been reported as feeding on Hop, *Humulus lupulus* L. (Theobald, 1925), of which about a dozen are macro-lepidoptera and two are butterflies – *Inachis io* L. and *Polygonia c-album* L. In addition to hop, in the wild the early stages of the Comma have been noted as feeding on stinging nettle (*Urticae dioica* L.), both common and wych elm (*Ulmus glabra* Hud. and *U. procera* Sal.), various currants (*Ribes* spp.), and rarely on Hornbeam (*Carpinus betulus* L.) and Hazel (*Corylus avellana* L.); other feral foodplants listed include raspberry, honeysuckle, thistle, sloe, and willow (Kirby, 1909).

An indeterminable amount of the distribution of hop is due to escapes from the brewing industry's early hop-gardens, although it is thought to be native in England and Wales; examination of the plants distribution (Perring & Walters, 1976) reveals a striking similarity with that of *c-album* when at the height of its range in this country. Almost all of the distribution of purely commercial hop-growing (Parker, 1934; Coppock, 1964) is within that of the Comma's – but when its range was most restricted; to a large extent this similarity also extends to Europe, although all these coincidences could be climatic.

Detailed histories of hop culture have been published (Parker, 1934; Mathias, 1959; Burgess, 1964). Hop was a naturalised growth by 1428 but in 1511, or 13 years later, plants were introduced from the continent for the then newly fashionable brewing of beer. It was to be almost half a century before hop-gardens spread rapidly but by 1573 it was an established branch of agriculture. The first gardens were established at Maidstone and Canterbury – Kent being geographically well situated because of its climate, soil, access to London dung and casual labour – and after about a decade in Norfolk, and later at Farnham and the Severn Valley. It was after the

late 16th century that the practise spread from the south-east to the midlands. The national acreage increased over the 17th century and picked hops arrived from Holland at this time and during the following century when large quantities were recorded. By 1724 the national area under hop totalled more than 23,000 acres with over three-quarters grown in Kent, Sussex, Worcestershire, Surrey, Hampshire, and Herefordshire; more than 5000 acres were grown outside of these six counties. During the 18th century 6000 acres were grown near Canterbury alone, although much was grubbed out in 1780, hops were planted in abundance in Herefordshire, and smaller amounts were successful in Nottinghamshire, Suffolk, and elsewhere in the west midlands; by 1776 the plant was even being experimented with in Scotland, although comparatively little was grown north of the Trent, and Farnham was called the first hop capital of Britain. But a decline in the acreage farmed outside of the six prime counties took place – by 1822 the area had more than halved and half a century later only a tenth of the original area still grew hops. Nevertheless in 1870 hops were still cultivated in 53 counties – 40 in England, eight in Wales, and five in Scotland – as far north as Aberdeenshire; but this was to be the peak as a dramatic drop in distribution immediately took place. At this time more than 99% of the country's total hop acreage was situated in the foremost six counties, with two-thirds in Kent. The last hops were grown in Scotland in 1871 and in Wales in 1874, then, "as the acreage fell away hops went out of cultivation almost entirely in all but the half-dozen counties" (Parker, 1934). Within these hop-growing heartlands the acreage peaked in 1878 at more than 71,000 acres; this slowly declined until 1887 when a sharper fall occurred, due to reduced demand and better yields through increased pest control. By 1909 the national acreage had halved and in 1917 had halved again. This depressed acreage of less than 20,000 acres has been maintained ever since. The future of the industry is currently under threat from a recent EEC ruling which allows "exposure to the rude gusts of market forces, world over-production and continental hops" (Sunday Times, 23/6/85); now, less than 8000 acres are cultivated in Kent and a third of the growers have gone out of business over the last decade.

Although imports had come from all over the continent and some of the British colonies of the era, the comparative quantitative distribution of commercially grown hops has changed little since the latter part of the 19th century; as at present, just before the Second World War about two thirds of the country's acreage was still grown in Kent and the far east of Sussex, with much of the remainder being situated in Herefordshire and Worcestershire. Of course, although the distribution and acreage of commercial hop-growing had collapsed, the plant was (and is) still widespread – but the

unusually advantageous opportunities for *c-album* had gone.

More than half of the hop varieties grown about 20 years ago were old established strains but changes in the remainder were most unlikely to have affected the Comma as all strains of hop are thought to be botanically inseparable.

There is no evidence to show that *c-album* was an economically serious pest on hop in this country over the last hundred years – although "thousands" of pupae were mentioned at a Leominster hop-garden in 1875 (Barrett, 1893). But there is no doubt that hop was the insects primary foodplant throughout most of the last century and just previously; Moses Harris (1770) wrote that the larvae "generally feeds on the leaves of hop, but is sometimes found on the nettle"; in the mid-19th century it was said that larvae fed on various plants "especially hops" (Westwood, 1854); towards the end of that century the celebrated Mrs. Hutchinson called it "very common in hopyards" in Herefordshire and at about the same time similar remarks were made about the Maidstone hop district (Newman, 1871). Later, Dale (1890) mentioned that second brood larvae "would appear to prefer hop" and that "when the hop-picking season comes on, the caterpillars and also the chrysalides are found in much larger numbers"; and the foremost authority of the era, Barrett (1893), agreed on the species foremost foodplant. But due to the decline of hop-culture, by the begining of the First World War no lesser an authority than Frohawk (1914) said that "it's chief and natural foodplant is the common stinging nettle"; this has recently been confirmed by modern observation (Heath *et al*, 1984). On occasion, hop will no doubt locally still be the species primary foodplant, although pesticides would now keep these occurrences to a minimum in the remaining hop-gardens; equally, there were places where probably stinging nettle was always to the fore, such as north Wales (see Gardner, 1913). Almost all authorities researched who defined the primary foodplant of the Comma before the turn of the century chose hop and the vast majority of those after that time chose the ubiquitous stinging nettle – and the individual records of discovered larvae confirm this statement. It has been suggested that larvae fed on different foodplants depending upon brood, where "the second brood would appear to prefer hop, but as that plant is scarcely in leaf when the first brood are feeding, the early caterpillars must of necessity find other food" (Dale, 1890) – this being currant and stinging nettle (Hutchinson, 1881).

There is some truth in the statement that "the Comma of older days was primarily a hop feeder, and that it disappeared through newer methods of hop spraying" (Lewis, 1951). As the acreage under hop increased after the late 16th century this no doubt led to an increasing incidence of associated insect pests,

which would have included *c-album*. The first mention of pest control on hops was as early as 1697 when it was recommended that plants should be sprinkled with an infusion of Wormwood. Much later, during the 1860's, dusting powders of soot and lime were used in an attempt to control flea beetle; at the same time sprays of soft soap and quassia extract began to be used – but the practise did not become general before 1883. After this time, insecticidal spraying prevented disastrous crop failures and contributed to the decline in acreage through increased yields. At the turn of the century at Malvern the butterfly was listed as "formerly plentiful in hop-yards, but since the introduction of "hop-washing" much less abundant, and probably still decreasing" (Edwards & Towndron, 1899). After the First World War it was said of lepidopterous larvae on hop that "damage is rarely important and they are much less common than they were before the widespread use of insecticides" (Burgess, 1964) and that larvae of the Comma were now only found on the plant "from time-to-time"; in other late books on the pests of hops the species is not even mentioned. In 1949 systemic insecticides such as Schradan were first introduced and these completely revolutionised pest control on hops. Therefore there will never be a return to those halcyon days when Mrs. Hutchinson had "about one thousand larvae and pupae brought me from the few hop-grounds in our parish" (Hutchinson, 1881) of Grantsfield, in 1875; nor even in Yorkshire, where previously the butterfly had been reported as "alighting in hundreds on the blossoms of the common wild Scabious" (Morris, 1870).

On occasion, there were direct losses from human intervention, as specimens were sometimes obtained "with difficulty, some enterprising collector having circulated advertisements in the local papers of the hop-growing districts in Herefordshire and Worcestershire, as well as posting placards in the villages, to offer to take all the larvae and pupae the hop-pickers could find, at a certain rate" (Buckler, 1886). However, the numbers enjoyed by *c-album* were sometimes so vast in these districts before pest control became efficient as to render these attentions negligible besides those of the hop-growers; as a measure against pests, there was a habit "of collecting all the bine after the gathering is over and burning it, and thus all the larvae and pupae which have not been destroyed, when the poles are torn down and the hops gathered, perish in the fire, excepting those which have emerged and thus escape destruction . . . it has been sad to see the destruction of larvae and pupae" (Hutchinson, 1881).

It has been suggested that, after the loss of a hop-feeding race due to changes in hop-spraying methods, the species "re-established itself through immigrants which were primarily elm feeders, dislodged from which they can usually find nettle" (Lewis,

1951). Part of this is not quite as controversial as might at first be thought, as it has been concluded of lepidoptera as a whole that "there may be two or more biological races within a single species, each race selecting a particular foodplant" (Allan, 1943). Also "when a species has been reared for several generations on one of several alternative host plants, the progeny will tend to select the same host plant on which they were reared . . . . it is also possible . . . that in any given species there may be many heterozygous strains with all the possible combinations of host plant preferences. If this is the case, there may be a selective action of the environment in eliminating all the progeny which have a tendency to choose other host plants than those upon which they hatch" (*loc. cit.*); it has been recorded that some species are unable to successfully complete there development after feeding readily on some alternative plants (Balfour-Browne, 1944). Local races of *c-album* have been reported; one feeding on nettle and another on sallow in Somerset (Heslop, 1967), and on stinging nettle in north Wales (Gardner, 1913). Nationally, however, as has been shown, the insect largely retreated to the midland hop-growing areas, regaining territory from these strongholds, and any later tendency in foodplant preference would therefore have been biased towards hop; internationally, vagrants apart, the case for the occurrence of arrivals from the continent, elm feeding or otherwise, is less than proven. However, as the Welsh experience shows, there were races which fed on stinging nettle when the insect was at its nadir in this country and it has been shown that there was a change in the foremost foodplant at about that time, brought about by the collapse of commercial hop-growing; whether the change was due to polyphagous *c-album* losing hop as a preferential opportunity, or became a change in dominence within monophagous races, either way the cause remains the same.

There is recent evidence of local changes in primary foodplant (Baker, 1977); stinging nettle was reportedly the foremost pabulum for the Comma in south London earlier this century but in nearby north-west Surrey it was discovered to be elm in 1969 – until Dutch Elm disease forced a change to sallow, hop, and gooseberry, during the 1970's. As the numbers of *c-album* were said not to have been affected, this shows that the species can have sudden changes in foodplant forced upon it in the wild, at least locally with those plants, without noticeable loss. Unless the predominence of an exclusively hop-feeding race is accepted, this runs contrary to any conclusions of widescale loss of territory due to the decline of hop-growing. Nevertheless, due to the mode and speed of loss of individual hop-gardens (grubbing up, virtually overnight) there can be little doubt that there were significant local numerical losses and perhaps even local extinctions from this cause.

Despite several statements to the contrary, such as "the cause of its disappearance cannot be associated with cultivation or with any other interference with its requirements" (Frohawk, 1914), hops were not grown commercially in Scotland after 1871 or in Wales after 1874; in England, outside of the prime hop growing counties the acreage declined throughout the 19th century and its distribution completely collapsed after 1870. The butterfly was last recorded in Scotland in about 1870 and it disappeared from an accelerating number of English counties during that same decade. Also, hop washing, bine burning, and the increasing deployment of more efficient pesticides after the early 1880's contributed to local rarity.

(*to be concluded*)

MUD-PUDDLING BEHAVIOUR OF THE GREEN-VEINED WHITE BUTTERFLY. — Mud-puddling behaviour is a well documented and common phenomenon of male butterflies of tropical and mediterranean regions, but is of less common occurrence in temperate regions. The principal stimulant to these male aggregations is described as sodium salt (Arms *et al., Science,* **185**: 372-374.) and large groups of males usually congregate and feed on damp ground contaminated by faeces and urine, presumably these areas are rich in available amino-acids.

On 5 August 1986 I was visiting a coniferous area of woodland in north Bucks., a sunny but cool day after an evening of very heavy rain. On one 300 metre length of ride I noted seven aggregations of feeding male green-veined white butterflies, at the edge of puddles. Each group of males was densely packed, with approximately one to five centimetres between individuals. The total number of males within each group were; 37, 21, 18, 17, 14, 13 and 6. No other aggregations of this butterfly were noted at any other puddles on this or any other ride. Close examination of the attractive and non-attractive puddle margins revealed no evident differences between the puddles themselves and no signs of faeces. However, those puddles that were attractive were all immediately adjacent to vegetation that had been mown within the previous week. Presumably the heavy rain of the previous evening had washed the soluble products of decomposition into these puddles, these being attractant to this butterfly. What is of interest is whether this is a rare phenomenon or is more common than generally believed. Also, is sodium salt involved in instances as described here? T. G. SHREEVE, 4 Chiltern Close, Princes Risborough, Aylesbury, Bucks. HP17 0EA.